

Obligatory Summer-Dormant Cool-Season Perennial Grasses for Semiarid Environments of the Southern Great Plains

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ABSTRACT

Introduced cool-season perennial grasses may become an important complementary winter forage to dual-use wheat (*Triticum aestivum* L.) in high-risk semiarid environments of the southern Great Plains. Currently recommended, summer semidormant cultivars are not adapted to prolonged and severe summer drought and not productive in the autumn grazing season. In an experiment planted at Vernon, TX, on a Miles fine sandy loam (fine-loamy, mixed, thermic Udic Paleustalfs) in October 2000, we evaluated productivity and plant survival of an obligatory summer-dormant 'Grasslands Flecha' and summer semidormant 'Georgia 5', 'Jesup', and 'Kentucky 31' tall fescue (*Festuca arundinacea* Schreb.); a highly summer semidormant 'Grasslands Maru' hardinggrass (*Phalaris aquatica* L.); and summer semidormant 'Grasslands Matua' and 'Grasslands Tango' prairiegrass (*Bromus willdenowii* Kunth) under two defoliation intensities of 7.5 and 15 cm. Georgia 5, Jesup, and Grasslands Flecha were either infected with the novel *Neotyphodium coenophialum* Glenn, Bacon, and Hanlin endophyte strain AR542, with their endemic endophytes (except for Grasslands Flecha), or noninfected (E-). Only Grasslands Flecha and Grasslands Maru successfully survived summer droughts during 2001–2004. Prairiegrass behaved as an annual but did not reseed in 2003. Aboveground biomass was greater at 15- vs. 7.5-cm defoliation height, except for 2004 growing season. In Grasslands Flecha, the novel endophyte increased tiller survival during summer drought by 150% (2001) and 121% (2002) when compared with E-plants. Obligatory and highly summer semidormant cultivars of perennial cool-season grasses may be productive and persistent in the southern Great Plains and have the potential to complement forage from dual-use wheat pastures.

THE BIMODAL PATTERN of precipitation, with peaks in May and September, severe water deficits accompanied by extreme heat in summer, and relatively mild winters, determines primary (forage) and secondary (animal) production from agroecosystems in the southern Great Plains. One of the most important crops adaptable to these environments is winter wheat cultivated on approximately 6.5 million ha (Pinchak et al., 1996). In Texas, Oklahoma, and portions of New Mexico, Kansas, and Colorado, wheat is a dual-use crop, providing both winter forage for cattle and a grain crop. Unpredictable autumn rain often delays planting of wheat, resulting in a lack of high quality forage for cattle to graze into the winter and early spring. Another gap in forage availability occurs in the southern Great Plains

from early March, when grazing on dual-use wheat must be terminated to produce grain crop, until May when grazing on warm-season perennial grass pastures can be initiated (Reuter et al., 1999).

Introduced cool-season perennial grasses are becoming an important source of high quality winter forage to complement or replace wheat forage and perennial warm-season grass pastures in the southern Great Plains (Reuter and Horn, 2002). Perennial cool-season grasses may potentially be a more reliable and economically sound source of early-season forage than wheat, saving farmers about \$100 per ha annually (Redmon, 1997). They also contribute to environmental sustainability of the agroecosystems by reducing water runoff and soil erosion (Brady and Weil, 1996), conserving soil water during summer drought (Hanselka et al., 1994), improving soil physical and chemical properties (Dormaer et al., 1995), and providing habitat for wildlife (Duebbert et al., 1981).

Severe and often prolonged summer droughts and poorly understood management practices adversely affect persistence and productivity of introduced cool-season perennial grassland ecosystems at the margin of their environmental adaptation in the southern Great Plains region (Redmon, 1997; Malinowski et al., 2003). All currently recommended varieties of cool-season perennial grasses (Alderson and Sharp, 1995) are summer semidormant, i.e., they cease growth in response to soil water deficits and high temperatures during summer (Cooper, 1963; Volaire, 1995). Summer semidormant grasses possess numerous mechanisms of drought avoidance (drought stress terminology after Levitt, 1980) to minimize the extent of tissue dehydration during summer drought by maintaining water uptake from deeper soil levels and limiting water loss via transpiration (Ludlow, 1989; Volaire et al., 1998). Defoliation stress combined with severe soil water depletion and high temperatures during summer dramatically reduce the persistence of cool-season perennial grasses in semiarid environments (Malinowski et al., 2003). As a result, introduced cool-season perennial grassland ecosystems are short-lived and require frequent re-establishment, which precludes their widespread use in the southern Great Plains (Redmon, 2000).

In contrast to summer semidormant types, numerous ecotypes of cool-season perennial grasses originating from the Mediterranean Basin become summer dormant in response to increasing daylength and probably high temperatures (Laude, 1953; Ofir and Kerem, 1982). This process, defined as obligatory summer dormancy, functions independently from soil moisture (Cooper,

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1963; Villiers, 1975). Based on such ecotypes, breeders in Argentina, Australia, Italy, and New Zealand have recently developed cultivars of cool-season perennial grasses that are persistent in environments with prolonged and severe summer droughts (Charlton and Stewart, 2000; McDonald, 2001; Piano et al., 2003). Although mechanisms of obligatory summer dormancy in cool-season perennial grasses are not well understood, a complete cessation of growth functions, except for shoot meristems or surviving vegetative structures like buds and bulbs, enables grass plants to *escape* (drought stress terminology after Arraudeau, 1989) summer drought and initiate autumn regrowth in response to decreasing daylength and lower temperatures (Laude, 1953; Ofir and Kerem, 1982; Oram, 1984; Ofir, 1986; Volaire and Thomas, 1995; Ofir and Kigel, 1999). These unique adaptations suggest that, in transitional semiarid steppe and warm semiarid steppe zones such as those of the southern Great Plains (Kephart et al., 1995), grasslands ecosystems with obligatory summer-dormant cool-season perennial grasses might be more persistent and sustainable than those based on summer semidormant cultivars (Knight, 1973; Ceccarelli and Somaroo, 1983; Volaire, 1994, 1995; Reed, 1996). Low autumn forage productivity, a characteristic of summer semidormant types, is the most limiting factor to economic returns from beef production systems in the southern Great Plains (Schuster et al., 1973). Aljoe (2002) estimated that 45 to 60 d of additional grazing and gain in late autumn to early winter would increase income by \$62 to \$75 per ha. With adequate precipitation, obligatory summer-dormant cool-season perennial grasses grow actively during winter and early spring in their native environments; thus, they appear better suited as complementary forages to dual-use wheat than currently cultivated, summer semidormant types.

Tall fescue is the most dominant cool-season perennial grass grown in the eastern and northwestern USA (Sleper and Buckner, 1995). It is also an important forage in eastern Oklahoma and northeastern Texas where annual precipitation is at least 750 mm (Hannaway et al., 1999). Most of the tall fescue pastures in the USA are infected by the symptomless fungal endophyte *Neotyphodium coenophialum* Glenn, Bacon, and Hanlin (Shelby and Dalrymple, 1987). The associations of tall fescue (and several other cool-season perennial grasses) with *Neotyphodium* spp. endophytes are defined as asymptomatic symbioses (Wilkinson and Schardl, 1997). Endophyte-infected (E+) grasses usually express superior growth, drought and mineral stress tolerance, and competitiveness than noninfected plants (Malinowski and Belesky, 2000). Endophyte infection stimulates the host grass plants to produce an array of bioprotective alkaloids (Porter, 1994; Bush et al., 1997) and nonalkaloid secondary metabolites (Ju et al., 1998) that increase resistance to biotic stresses. In tall fescue, production of ergot alkaloids by E+ plants has been related to health disorders in grazing animals called "fescue toxicity" (Bacon et al., 1977; Hill et al., 1994). Introduction of E- tall fescue varieties has not been successful to date because of their poor persistence once exposed to

abiotic stresses (Bouton, 2001). More promising approaches include genetic manipulation of *Neotyphodium* spp. endophytes (Schardl, 1994) or isolation of naturally occurring, non-ergot-producing strains and re-infecting elite varieties with them (Siegel and Bush, 1994). One such novel endophyte is the strain AR542 selected in New Zealand (Latch et al., 2000), which has been reinfected into tall fescue varieties Jesup and Georgia 5 (Bouton et al., 2001) and commercialized by Pennington Seed, Inc. (Madison, GA) as the MaxQ technology.

We hypothesized that obligatory summer-dormant cool-season perennial grasses may be more drought resistant than their summer semidormant counterparts in the Texas Rolling Plains, one of the driest and hottest regions of the southern Great Plains. Novel fungal endophyte strains may further increase the persistence of tall fescue, similar to wild-type endophyte strains. The objectives of this study were to (i) determine persistence and forage productivity of perennial cool-season grasses with contrasting types of summer dormancy and (ii) determine the role of wild-type and novel endophytes on tall fescue drought tolerance.

MATERIALS AND METHODS

Obligatory summer-dormant tall fescue was represented by cultivar Grasslands Flecha¹ [Gentos SA (Buenos Aires, Argentina) and AgResearch Grasslands (Palmerston North, New Zealand)]. Grasslands Flecha is a Mediterranean-type cultivar with highly active winter growth. Summer semidormant tall fescue varieties were represented by Jesup and Georgia 5, bred for more pronounced summer growth (Bouton et al., 1993, 1997), and Kentucky 31, the original tall fescue variety released by the Kentucky Agricultural Experiment Station in 1942 (Alderson and Sharp, 1995). Highly summer-dormant hardinggrass was represented by cultivar Grasslands Maru (AgResearch Grasslands, Palmerston North, New Zealand). Grasslands Maru is a Mediterranean-type cultivar with a high level of summer dormancy, active winter growth, and marginal levels of dimethyltryptamine alkaloids and cyanogenic glycosides (Stevens et al., 1989). Prairiegrass cultivars Grasslands Matua, released in 1973 by New Zealand's Department of Scientific and Industrial Research-Grasslands Division (Rumball, 1974), and Grasslands Tango (Gentos SA/AgResearch Grasslands) were chosen as check cultivars.

Grasslands Flecha tall fescue was either E- or reinfected with the novel, nontoxic AR542 strain of *N. coenophialum*. Jesup and Georgia 5 were E-, infected with their wild-type, ergot-producing endophyte strains (WT) or reinfected with the nontoxic AR542 strain (Jesup MaxQ and Georgia 5 MaxQ). Kentucky 31 was infected with a wild-type, ergot-producing endophyte strain. Endophyte infection rate in seeds was not less than 96% (immunoblot test).

Plots (1.8 by 10 m) were established at Vernon, TX, on a Miles fine sandy loam (fine-loamy, mixed, thermic Udic Paleustalfs) on 30 Oct. 2000. Initial soil pH was 6.6, with adequate concentrations of P (20 mg kg⁻¹) and K (300 mg

¹ Seeds of Jesup MaxQ and Georgia 5 MaxQ tall fescue were supplied by Pennington Seed Inc.; Jesup E- and WT, Georgia t E- and WT, and Kentucky 31 tall fescue by the University of Georgia; and Grasslands Flecha (E- and infected with the AR542 *N. coenophialum* endophyte strain), Grasslands Matua, and Grasslands Tango prairiegrass and Grasslands Maru hardinggrass by AgResearch (USA) Ltd.

kg⁻¹). Before planting, plots were fertilized by deep placement of 45 kg N ha⁻¹ as liquid NH₄NO₃. Seeds were planted with a Hege 1000 small-plot planter (Hege Equipment, Inc., Colwich, KS) in tilled soil at row spacing of 0.25 m and seeding rate of 22 kg ha⁻¹ (tall fescue), 33 kg ha⁻¹ (prairiegrass), or 6 kg ha⁻¹ (hardinggrass) pure live seeds. Plots were broadcast-fertilized with 45 kg N ha⁻¹ as (NH₄)₂SO₄ in March and November during 2001–2004. Broadleaf weeds were controlled with met-sulfuron {methyl 2-[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)-amino]carbonyl]-amino]-sulfonyl]benzoate} at the rate of 2.02 g a.i. ha⁻¹ in May 2001 and 2002.

The experiment was a split-plot design in a randomized block design with four replicates. Grass cultivars containing endophyte treatments were planted in strips as whole plots with combinations of defoliation intensity imposed as subplots. Subplots, 1.8 by 5 m in size, were defoliated between 8 April and 12 June 2001 (two harvests of tall fescue cultivars, three harvests of Grasslands Maru hardinggrass, and three harvests of prairiegrass cultivars), 12 April and 4 June 2002 (four harvests of Grasslands Flecha tall fescue, three harvests of Grasslands Maru, and three harvests of prairiegrass cultivars), 1 April and 16 June 2003 (two harvests of all surviving cultivars), and 19 April and 6 June 2004 (three harvests of all surviving cultivars) by clipping at a height of 7.5 or 15 cm when swards reached 25-cm height. Defoliation was initiated in each growing season when inflorescence emerged. For this experiment, growing season is defined as the period from October through mid-June. Subplots were defoliated mechanically with the exception of a 0.5-m² area that was hand-harvested to determine dry matter (DM) content.

At the end of each growing season, a 0.25-m² section of each defoliated subplot was harvested to the ground level for stubble DM determinations. In each year, stubble was collected from a different section of a subplot to minimize carryover effects. Aboveground biomass was the sum of cumulative herbage DM yield and stubble DM below the defoliation height. The number of live tillers (at least one green leaf present) was recorded before the onset of summer drought (June 2001, July 2002, July 2003, and June 2004) and after summer drought (December 2001, November 2002, and November 2003) by counting tillers from a 0.3-m section of one row in the middle of each subplot.

Data were analyzed using PROC MIXED procedure of SAS (Littell et al., 1996). Replications were considered random, whereas cultivars, endophyte status (where appropriate), defoliation intensity, and growing season were considered fixed factors. The effects of infection with AR542 endophyte strain on aboveground biomass and tiller number were analyzed for Grasslands Flecha, Georgia 5, and Jesup while effects of AR542 vs. wild-type endophyte strains were analyzed for Georgia 5 and Jesup. Mean separation was performed using the protected least square means (LSMEANS) procedure. Significance was declared at $P < 0.05$.

RESULTS

Weather Patterns

After planting in October 2000 until December 2000, average monthly temperatures were about 3°C below (Fig. 1A) and precipitation was 160% above the long-term averages (Fig. 1B). Under such conditions, seedling establishment was successful. During January 2001 until June 2001 (beginning of summer drought), average temperatures and precipitation patterns were near normal for this region. Summer drought of 2001 was severe,

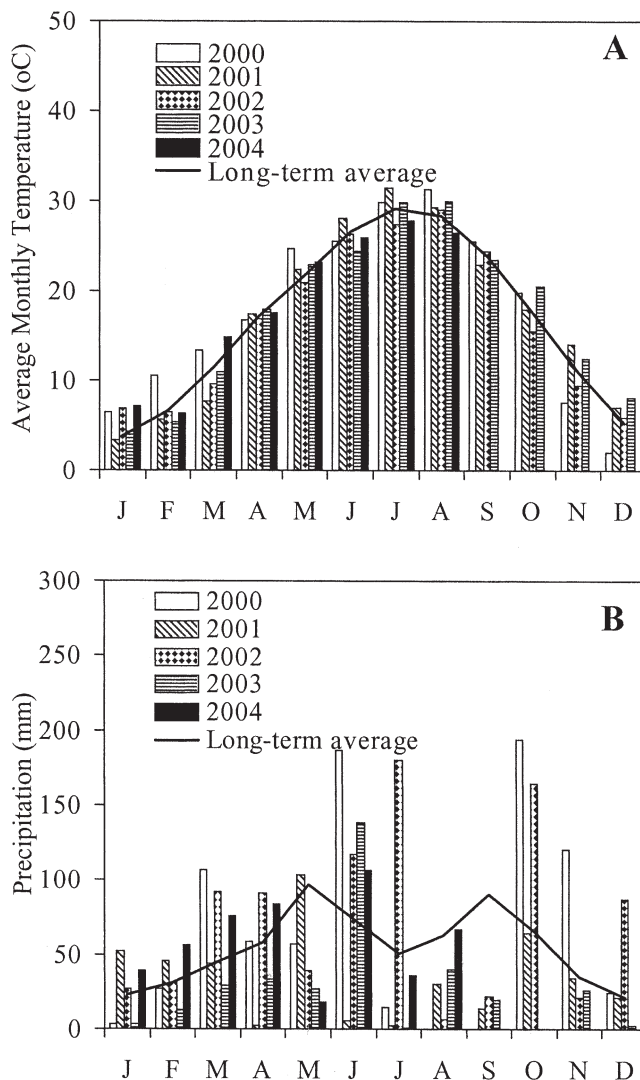


Fig. 1. (A) Average monthly temperature and (B) precipitation at the experimental location in Vernon, TX, during 2000–2004 (August).

following the pattern of the last 3 yr, and characterized by higher-than-normal temperatures (1.5, 2.3, and 0.9°C above average for June, July, and August, respectively) and only 21% of the long-term average precipitation. Severe drought extended through November 2001. Average monthly temperatures and precipitation during January through May 2002 were close to the long-term averages. In contrast to 2001, average monthly temperatures for June and July 2002 were 0.2 and 1.7°C below the long-term average, and precipitation was 159 and 358% greater than the average. August and September 2002 were very dry (11 and 24% of the long-term precipitation, respectively), followed by relatively normal precipitation pattern during October through December 2002. Extreme winter-through-spring drought occurred in 2003, with precipitation reaching only 42% of the long-term average during January through May. The drought continued throughout the rest of the year, with only 56% of the long-term average precipitation during June through December. During early spring to early summer 2004, precipitation (except for May) was above and temperature close to long-term averages.

Table 1. Seedling weight of grass cultivars determined 37 d after planting.

Species	Cultivar	Seedling weight
		mg
Tall fescue	Grasslands Flecha	2.01 cd†
	Georgia 5	2.38 c
	Jesup	2.45 c
	Kentucky 31	1.89 cd
	Grasslands Maru	1.62 d
Hardinggrass	Grasslands Matua	9.35 a
Prairiegrass	Grasslands Tango	6.41 b

† Means followed by the same letter (columns) are not significantly different at the 0.05 probability level.

Seedling Dry Matter

Seedling biomass (root and shoot DM) was determined on 7 Dec. 2000, i.e., 37 d after planting, to help explain differences in grass cultivar persistence and the effect of endophyte strain on tall fescue vigor. Grasslands Matua and Grasslands Tango prairiegrass had seedling with the greatest ($P < 0.05$) biomass, followed by tall fescue cultivars and Grasslands Maru hardinggrass (Table 1). Wild-type and AR542 endophyte strains did not affect seedling biomass of tall fescue that ranged from 2.23 to 2.41 g.

Aboveground Biomass Production

There were significant interactions between growing season and grass cultivar as well as growing season and defoliation height on aboveground biomass (Table 2). Biomass data for tall fescue/endophyte associations were pooled within each tall fescue cultivar for this analysis. During spring 2001 (first growing season), Grasslands Tango and Grasslands Matua prairiegrass produced the greatest aboveground biomass followed by Georgia 5 and Jesup tall fescue, Grasslands Maru hardinggrass, and Grasslands Flecha and Kentucky 31 tall fescue (Table 2). Intensive vs. extensive defoliation reduced aboveground biomass in all cultivars in the first

three growing seasons but did not affect aboveground biomass in 2004 (Table 2). Summer semidormant tall fescue cultivars died during the first summer drought, regardless of defoliation treatments. In the second growing season (2002), prairiegrass and Grasslands Flecha tall fescue produced more aboveground biomass than Grasslands Maru hardinggrass, but the order of productivity reversed in the third growing season (2003). Grasslands Maru and Grasslands Flecha recovered well from 2003 drought stress and produced similar (Grasslands Flecha) or about 170% greater (Grasslands Maru) biomass in 2004 vs. 2002 growing season.

Averaged for Georgia 5 and Jesup tall fescue, plants infected with AR542 endophyte strain produced about 16% less aboveground biomass than E- plants or plants infected with their endemic strains in the first growing season (Fig. 2A). In contrast, infection with AR542 endophyte did not affect aboveground biomass in Grasslands Flecha in the first three growing seasons but increased biomass production by 122% in the fourth growing season (after an extremely dry year of 2003), regardless of defoliation height (Fig. 2B).

Tiller Dynamics and Summer Drought Survival

Georgia 5, Jesup, and Kentucky 31 tall fescue had the greatest tiller numbers at the end of the first growing season (1673–1971 tillers m^{-2}), followed by Grasslands Flecha (1385 tillers m^{-2}), while Grasslands Tango and Grasslands Matua prairiegrass and Grasslands Maru hardinggrass had the lowest tiller numbers (816–905 tillers m^{-2}). Only Grasslands Flecha tall fescue (obligatory summer-dormant type) and Grasslands Maru hardinggrass (highly summer semidormant type) recovered from summer drought in 2001 although only 48 and 70% tillers, respectively, survived. Tillers of all other cultivars died. Swards of Grasslands Matua and Grasslands Tango prairiegrass re-established from seeds in

Table 2. Aboveground biomass produced by grass cultivars in response to defoliation height at the end of each growing season (June) during 2001–2004.

Grass species/ defoliation height	Cultivar	Aboveground biomass			
		2001	2002	2003	2004
		kg ha ⁻¹			
Grass species Tall fescue	Grasslands Flecha	2437 c† B‡	4740 a A	1057 b C	4680 b A
	Georgia 5	3398 b	–	–	–
	Jesup	3382 b	–	–	–
	Kentucky 31	2405 c	–	–	–
	Grasslands Maru	2515 c C	3924 b B	1593 a D	6716 a A
Hardinggrass Prairiegrass	Grasslands Matua	4546 a A	4875 a A	1109 b B	–
	Grasslands Tango	4558 a A	4972 a A	1108 b B	–
Defoliation height	7.5 cm	3053 b C	3891 b B	1115 b D	5340 a A
	15 cm	3588 a B	5365 a A	1318 a C	6056 a A
	Source of variation	PROC MIXED			
	Growing season (Y)	*			
	Cultivar (C)	*			
	Y × C	*			
	Defoliation height (H)	*			
	Y × H	*			
	C × H	NS			
	Y × C × H	NS			

† Means followed by the same regular letter (columns) are not significantly different at the 0.05 probability level.

‡ Means followed by the same capital letter (rows) are not significantly different at the 0.05 probability level.

the early spring in 2002 and 2003, but no reseeding occurred in early spring of 2004 after severe summer and winter drought in 2003, and these cultivars disappeared from the plots (Fig. 3). Defoliation intensity did not affect the number of living tillers at the end of each growing season (June) and after summer drought (December) in Grasslands Maru hardinggrass and Grasslands Matua and Grasslands Tango prairiegrass. Grasslands Flecha tall fescue had more surviving tillers in response to less intensive defoliation after 2002 summer drought (December 2002), but the number of surviving tillers was not affected by defoliation intensity in other years (Fig. 3).

Regardless of defoliation height, infection with either the novel endophyte AR542 or endemic endophytes did not affect living tiller numbers of Georgia 5 and Jesup tall fescue before summer drought 2001 (1722–1912 tillers m^{-2}). Similarly, AR542-infected Grasslands Flecha did not differ in living tiller numbers from E- plants before summer drought in each year, but tiller survival

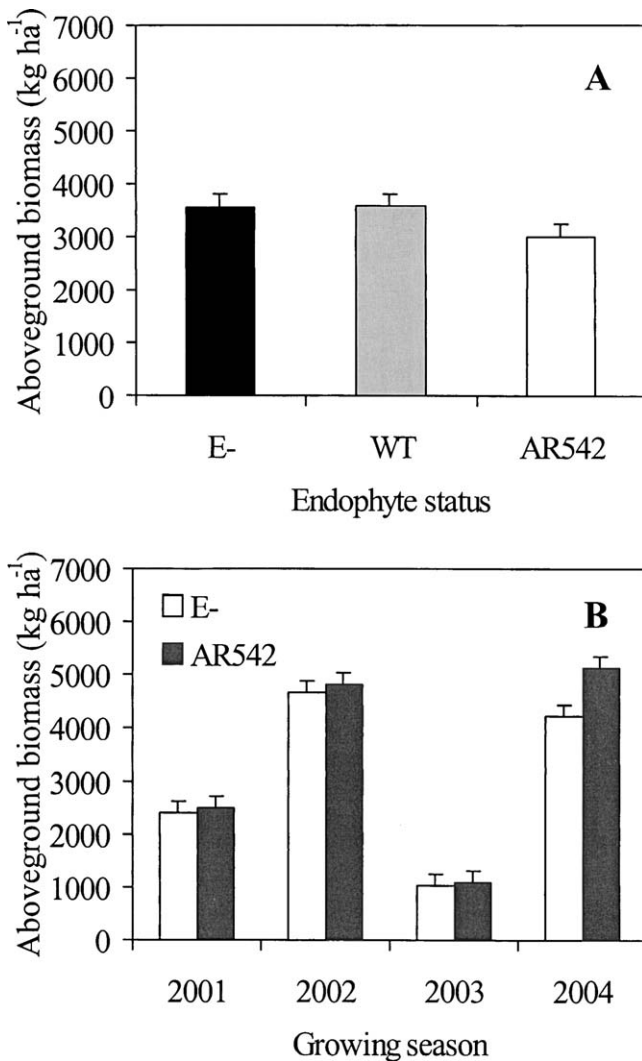


Fig. 2. Aboveground biomass production as a function of endophyte infection in (A) Georgia 5 and Jesup (averaged for both cultivars) in the first growing season and in (B) Grasslands Flecha tall fescue in 2001–2004 growing seasons. Bars indicate \pm 1 S.E. E-, noninfected; WT, infected with wild-type (endemic) endophyte strains.

during summer drought was greater in AR542-infected vs. E- plants after summer drought in 2001 and 2002 (Fig. 4).

DISCUSSION

We present the first evidence that obligatory summer-dormant tall fescue cultivar Grasslands Flecha is drought resistant in environments of the Texas Rolling Plains that are beyond the adaptation range of currently utilized, summer semidormant tall fescue types. A highly summer semidormant hardinggrass cultivar, Grasslands Maru, also appears to be persistent in these environments.

Aboveground biomass production of Grasslands Flecha tall fescue and Grasslands Maru hardinggrass during the first and second growing seasons was comparable or greater than that reported for wheatgrasses grown in the same environment (Malinowski et al., 2003). Aboveground biomass production was greater during the second vs. first growing season by 195 and 156%, respectively, for Grasslands Flecha and Grasslands Maru. In 2003, forage production declined when compared with previous 2 yr. This was a result of a severe precipitation deficit during the growing season before summer drought, as well as the rest of the year, a climatic phenomenon that last occurred in this area in 1917 (TCEQ, 2004). These extreme conditions affected tall fescue to a greater extent than hardinggrass (80 and 60% decrease in aboveground biomass production when compared with that in 2002, respectively). Both grasses, however, recovered biomass production during 2004 growing season. In three of the four growing seasons, more aboveground biomass was produced with less intensive defoliation, a typical response of cool-season perennial grasses grown in semiarid environments (Malinowski et al., 2003).

Superior persistence of obligatory summer-dormant vs. summer semidormant types of cool-season grasses has been proven in semiarid environments with Mediterranean-like summer drought (Reed, 1996; Anderson et al., 1999; Piano et al., 2003). In environments with pre-

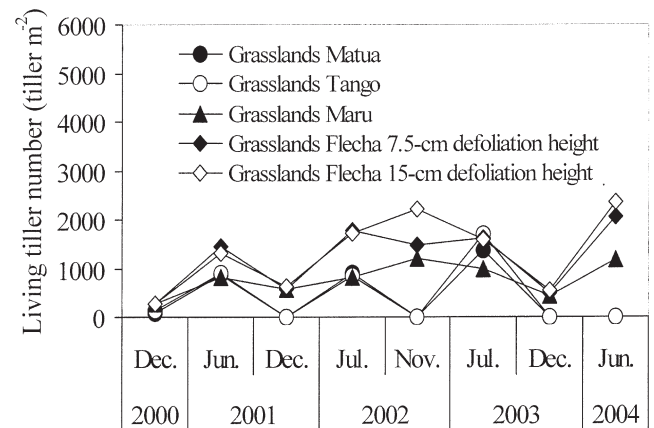


Fig. 3. The number of surviving tillers of Grasslands Matua and Grasslands Tango prairiegrass, Grasslands Maru hardinggrass, and Grasslands Flecha tall fescue before (June) and after (December) summer drought during 2001–2004. Except for Grasslands Flecha, data were pooled for defoliation height. Bars indicate \pm 1 S.E.

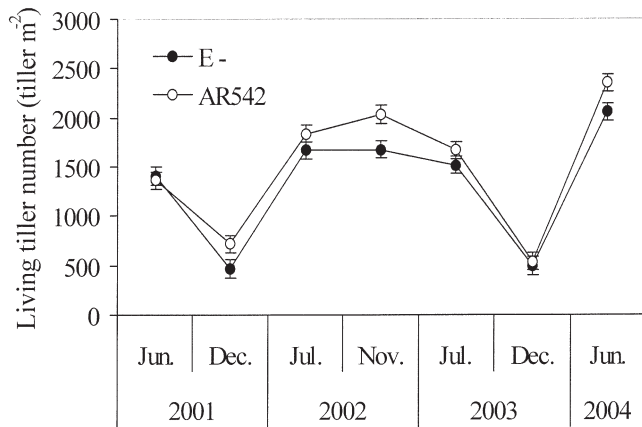


Fig. 4. The number of living tillers of Grasslands Flecha tall fescue in response to infection with the novel endophyte strain AR542 before (June–July) and after (December) summer drought during 2001–2004. Data were pooled for defoliation height. Bars indicate ± 1 S.E. E–, noninfected.

precipitation amounts during summer months adequate for survival of semidormant tall fescue types, the potential of obligatory summer-dormant types may not be fully evidenced. For example, Macoon et al. (2003) reported comparable forage production from Grasslands Flecha, labeled in their experiment as AGRFA 103 and AGRFA 110, with other tall fescue cultivars in the first growing season but lower production in the second growing season and similar persistence among all cultivars in central Mississippi. Similarly, the obligatory summer-dormant cultivar Resolute was one of the least-productive tall fescue cultivars in the first (2001) and second (2002) growing season at Lexington, KY (Spitaleri et al., 2003).

The number of living tillers before and after summer drought, except for Grasslands Flecha in 2002, was not affected by defoliation intensity. This, in part, agrees with results by Malinowski et al. (2003), who found that numbers of living tillers of wheatgrass species and varieties grown in the same environment were not affected by defoliation intensity before summer drought in the first growing season. The 7.5- vs. 15-cm defoliation height stimulated tiller survival in crested and pubescent wheatgrasses and tiller production of all wheatgrasses during the second growing season. In our experiment, in contrast, Grasslands Flecha and Grasslands Maru had more regrowing tillers in swards defoliated at 15- vs. 7.5-cm height after summer drought 2002 (beginning of the third growing season), and both cultivars had greater numbers of living tillers after summer drought when compared with tiller numbers before summer drought. This suggests that severity of summer drought may interact with defoliation regimes in determining tiller survival of obligatory or highly summer semidormant cool-season grasses as it affects semidormant types (Volaire, 1994; Boschma and Scott, 2000). In contrast to 2001 and 2003, the excessive precipitation in June and July 2002 followed by extended period of drought until October could have a detrimental effect on tiller dormancy and regrowth in intensively vs. extensively defoliated swards of Grasslands Flecha (Boschma and Scott, 2000). In contrast to Grasslands Flecha tall fescue, Grasslands

Maru hardinggrass is a highly summer semidormant type (not an obligatory summer-dormant grass); thus, regrowing tillers in autumn 2002 could have originated not only from dormant buds, but also from surviving tillers produced in the previous growing season (Oram, 1984).

Not all tillers of Grasslands Flecha tall fescue and Grasslands Maru hardinggrass survived the severe summer drought of 2001 and 2003. Grasslands Flecha had greater tiller mortality (57 and 68% in 2001 and 2003, respectively) than Grasslands Maru (30 and 56%). Both species, however, had the ability to recover tillers during growing seasons and produce about 1300 to 2200 (Grasslands Flecha) and 800 to 1000 (Grasslands Maru) living tillers m^{-2} each year before the onset of summer drought. Such ability to recover tillers after summer drought was not observed in a range of introduced wheatgrass species (summer semidormant grasses) evaluated in the same environment during 1998–2000 (Malinowski et al., 2003). Differences in tiller survival potential between obligatory summer-dormant tall fescue and highly summer semidormant hardinggrass may be related to strategies of summer drought survival developed in these grasses (Reed, 1996). Hardinggrass forms underground tuberous structures (buds) at the base of each tiller in early spring. These dormant buds survive summer drought and give a start to new tillers in autumn (McWilliam and Kramer, 1968). In tall fescue, the surviving organs are meristematic tissues, most likely protected from desiccation by senescent leaf sheaths. At the present time, it is not known what mechanism(s) regulates tiller meristem survival in obligatory summer-dormant tall fescue during summer drought.

Tillers of Grasslands Matua and Grasslands Tango prairiegrass were not able to survive summer drought, and both cultivars behaved as annuals, successfully recovering from seed each autumn, except for 2003 when they did not reseed and disappeared. Although prairiegrass has a more extensive root system than tall fescue (Shaffer et al., 1994), this may not contribute to tiller survival during summer drought in our environment. The annual growth characteristic of prairiegrass, therefore, will have implications for management practices that ensure adequate seed production before the onset of summer drought (Bell and Ritchie, 1989). The persistence of Grasslands Tango was not superior to that of Grasslands Matua under the conditions of our experiment.

Across tall fescue cultivars, neither the AR542 nor wild-type endophyte strains affected seedling DM when compared with E– plants. Endophyte infection may increase seed germination rate and seedling DM in some grass hosts (Clay, 1987), but this response depends on mineral (N) availability in soil (Cheplick et al., 1989). In other associations, host plant growth can actually be restricted in the presence of artificially introduced *N. coenophialum* strains (Hill et al., 1996), suggesting host/endophyte incompatibility (Christensen, 1995). The strain AR542 has been introduced to numerous tall fescue cultivars (Bouton, 2001; Wheatley et al., 2003) and seems to be highly compatible with them. In our

study, however, infection with the AR542 strain reduced total aboveground biomass in Georgia 5 and Jesup when compared with E- and WT-infected plants during the first growing season, regardless of defoliation intensity. Because these varieties did not survive summer drought, it could not be concluded if the reduction in aboveground biomass in AR542-infected plants was a season-specific phenomenon or had long-term implications. Wheatley et al. (2003) reported data suggesting positive effects of infection with the AR542 strain on herbage production in a range of tall fescue cultivars; however, the magnitude of these differences could be related to insect damage of E- plants. For the Grasslands Flecha tall fescue, infection with the AR542 endophyte strain did not affect total aboveground biomass production in the first three growing seasons but increased biomass production in the fourth growing season after an extremely dry year of 2003. AR542-infected Grasslands Flecha had a greater number of surviving tillers after summer drought in 2001 and 2002 when compared with E- plants. Similar effects of infection with wild-type endophyte strains on tiller survival were reported by numerous researchers in the past (reviewed in West, 1994). The novel endophyte strain AR542, thus appears to increase tall fescue persistence as efficiently as the wild-type, ergot-producing strains (Bouton et al., 2000).

Obligatory summer-dormant cool-season perennial grasses are better adapted to severe and prolonged summer droughts than currently recommended, summer semidormant cultivars, expanding the traditional range of cool-season grass adaptation in semiarid environments (Easton et al., 1994; McDonald, 2001; Piano et al., 2003). Introducing these grasses to pastures of the Texas Rolling Plains may result in a significant reduction of costs related to frequent renovation of cool-season perennial grass pastures in drought-prone environments (Oram and Lodge, 2003) and increase sustainability of grassland ecosystems in these high-risk environments.

ACKNOWLEDGMENTS

We thank Matt Angerer (TAMU Res. Ext. Cent., Vernon, TX) for technical support. We appreciate comments by Dr. Nicholas S. Hill (Univ. of Georgia, Dep. of Crop and Soil Sci., Athens, GA) and Dr. Larry A. Redmon (Texas A&M Univ., Dep. of Soil and Crop Sci., Overton, TX) on an earlier version of the manuscript and valuable suggestions by anonymous reviewers. This research was sponsored in part by AgResearch (USA) Limited (Asheville, NC).

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